

FORAGING-HABITAT SELECTION OF BLACK-BACKED WOODPECKERS IN FOREST BURNS OF SOUTHWESTERN IDAHO

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Abstract. We examined foraging-habitat selection of Black-backed Woodpeckers (*Picoides arcticus*) in burned forests of southwestern Idaho during 2000 and 2002 (6 and 8 years following wildfire). This woodpecker responds positively to large-scale fire disturbances and may be at risk from logging and post-fire management. With 100 radio-locations of four adult males, we used resource-selection probability functions in logistic form in an information-theoretic framework to model the Black-backed Woodpecker's selection of foraging habitat at fine and coarse spatial scales. Fine-scale data included characteristics of the foraging tree (tree level) and local habitat surrounding foraging trees (plot level, 0.04 ha), whereas coarse-scale data (224–778 ha) included patch characteristics within home ranges. Model selection by Akaike's information criterion identified a multi-scale model containing tree- and plot-level covariates, and their interaction, as the best model to characterize foraging trees. The positive effect of interaction between foraging-tree diameter and plot-level tree density suggested that foraging Black-backed Woodpeckers select both patches with dense trees and larger-diameter trees. Fire severity was not important, possibly because of the time since fire and the birds' habit of foraging on recently dead trees in adjacent unburned forests. Salvage logging that retains large-diameter trees in clumped distributions is most likely to provide long-term foraging habitat for Black-backed Woodpeckers in dry coniferous forests of the interior western U.S. Following wildfire, conservation of forest patches containing weakened trees may extend the suitability of habitat for foraging Black-backed Woodpeckers by up to 8 years.

Key words: Black-backed Woodpecker, foraging habitat selection, Idaho, *Picoides arcticus*, remote sensing, resource-selection probability function, wildfire.

Selección de Hábitat de Forrajeo de *Picoides arcticus* en Sitios Quemados de Bosque en el Sudoeste de Idaho

Resumen. Examinamos la selección de hábitat de forrajeo de *Picoides arcticus* en bosques quemados del sudoeste de Idaho durante 2000 y 2002 (6 y 8 años posteriores al incendio). Esta especie respondió positivamente a los disturbios de gran escala generados por el incendio y puede estar en riesgo por el manejo maderero y el manejo posterior al incendio. Con 100 localizaciones de radio de cuatro adultos macho, utilizamos formas logísticas de funciones de probabilidad de selección de recursos en un marco teórico de la información para modelar la selección del hábitat de forrajeo de *P. arcticus* a escalas espaciales finas y gruesas. Los datos a escala fina incluyeron las características del árbol usado para forrajear (nivel de árbol) y del hábitat local que rodea los árboles de forrajeo (nivel de parcela, 0.04 ha), mientras que los datos a escala gruesa (224–778 ha) incluyeron las características de los parches dentro de los rangos de hogar. La selección del modelo dada por el criterio de información de Akaike identificó un modelo de múltiples escalas que contuvo covariables a escala de árbol y parcela y sus interacciones como el mejor modelo para caracterizar los árboles de forrajeo. El efecto positivo de la interacción entre el diámetro del árbol de forrajeo y la densidad de árboles a escala de parcela sugieren que los individuos de *P. arcticus* que forrajean seleccionan parches densos de árboles y árboles con mayores diámetros. La severidad del incendio no fue importante, posiblemente debido al tiempo desde el incendio y al hábito de las aves de forrajear en árboles muertos recientemente en bosques adyacentes no quemados. Prevenir el aprovechamiento forestal de modo que perduren árboles de gran diámetro en altas densidades ofrece una buena oportunidad de brindar hábitats de forrajeo al largo plazo para *P. arcticus* en bosques secos de coníferas del interior oeste de EEUU. Con posterioridad a los incendios forestales, la conservación de parches de bosque que contengan árboles debilitados puede extender hasta 8 años la aptitud del hábitat para el forrajeo por parte de *P. arcticus*.

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INTRODUCTION

Black-backed Woodpecker (*Picoides arcticus*) populations are known to irrupt locally following large-scale forest disturbance (West and Speirs 1959, Wickman 1965, Lester et al. 1980), especially stand-replacing fire (Hannon and Drapeau 2005, Saab et al. 2005). However, irruptions following wildfire are usually temporary and populations decline within 2–4 years as food availability decreases (Murphy and Lehnhausen 1998, Saab et al. 2007, Nappi and Drapeau 2009). Between fires, Black-backed Woodpeckers are thought to persist in lower numbers in mature unburned forests (Nappi and Drapeau 2009, Tremblay et al. 2010). Because of the close association with their prey, primarily bark and wood-boring beetles (Scolytidae, Cerambycidae, and Buprestidae; Beal 1911, Murphy and Lehnhausen 1998, Powell 2000), Black-backed Woodpeckers are closely associated with recently burned habitats (Dixon and Saab 2000, Hoyt and Hannon 2002, Hutto 2008). Consequently, they may be vulnerable to post-fire salvage logging that reduces or eliminates high-quality habitats (Murphy and Lehnhausen 1998, Saab et al. 2007, Nappi and Drapeau 2009).

Previous studies suggest that the Black-backed Woodpecker's foraging behavior varies, although with some patterns regarding the use of specific trees, mode of foraging, and prey selection (e.g., Harris 1982, Villard and Beninger 1993, Tremblay et al. 2010). Regardless of habitat (e.g., burned, unburned, beetle-killed forest), Black-backed Woodpeckers forage predominantly in recently dead or dying trees of large diameter (Murphy and Lehnhausen 1998, Powell 2000, Nappi et al. 2003, Tremblay et al. 2010). Furthermore, although the dominant mode of foraging (e.g., scaling vs. drilling) varies with tree species, Black-backed Woodpeckers consistently prefer as prey wood-boring beetles over bark beetles (Bull et al. 1986, Murphy and Lehnhausen 1998, Powell 2000). Most studies report consistent use of the lower-to-middle portions of tree trunks and large-diameter logs with little decay (Goggans et al. 1989, Villard 1994, Murphy and Lehnhausen 1998, Tremblay et al. 2010). In recently burned forests (≤ 10 years after fire; Hutto 1995), Black-backed Woodpeckers generally select large-diameter trees scorched lightly to moderately (but occasionally heavily) (Caton 1996, Murphy and Lehnhausen 1998, Hoyt 2000, Hanson and North 2008). In boreal forests of eastern North America, Nappi et al. (2003) found crown condition (a measure of snag deterioration due to fire) to be the best predictor of high-quality foraging snags and large-diameter snags to contain higher densities of wood-boring beetles.

Resource selection, or the process by which an animal chooses its resources, is commonly described to occur in a hierarchical framework (Johnson 1980, Hutto 1985). Selection first begins at the broader, geographic range of a species, then progresses sequentially to finer scales and more precise habitat features. It is important to note that the criteria for selection may be different at each level and may carry different

associated costs and benefits (Johnson 1980, Hutto 1985). In recent years, habitat-selection studies have developed from single-scale analyses to multiscale approaches, in which habitat relationships among scales are considered simultaneously (Battin and Lawler 2006, Zimmerman et al. 2009). With a multiscale approach, investigators are now able to consider inherent cross-scale correlations between habitat features (Kristan 2006).

Most studies have characterized the Black-backed Woodpecker's foraging habitats at tree-level or fine spatial scales, whereas little work has been done at coarser spatial scales or has included multiple spatial scales (Goggans et al. 1989, Powell 2000, Hoyt and Hannon 2002, Tremblay et al. 2009). Results of multi-scale studies in unburned eastern boreal forests suggest that breeding Black-backed Woodpeckers establish home ranges in forests with a high proportion of recently cut patches and select patches of old coniferous forest as preferred foraging sites (Tremblay et al. 2009). In burned mixed-conifer forests in Montana, Black-backed Woodpeckers choose foraging locations with high density of prey at the level of the individual tree and select habitat at the patch level by other factors (Powell 2000).

We modeled selection of foraging habitat at fine and coarse spatial scales. The fine scale included the foraging tree (tree level) and local habitat characteristics surrounding foraging trees (plot level, 0.04 ha), while the coarse, remotely sensed scale (224–778 ha) included patch characteristics within home ranges. Our objective was to model the probability of a Black-backed Woodpecker foraging in a tree in burned forest as a function of fine-scale, field-collected data and coarse-scale, remotely sensed data. We used results from previous studies to make predictions regarding foraging habitat selection (e.g., Bull et al. 1986, Powell 2000, Nappi et al. 2003, Saab et al. 2009). We hypothesized that factors related to decline or mortality of trees should promote successful colonization of bark and wood-boring beetles and thus provide suitable habitats for foraging Black-backed Woodpeckers. We predicted that foraging habitats should consist of large-diameter charred trees, surrounded by high densities of ponderosa pines (*Pinus ponderosa*) that occur in large patches. We predicted these patches to have been burned more severely and be closer to patches at which crown closure was moderate to high pre-fire than were random locations.

METHODS

STUDY AREA

The study area had been burned in two adjacent wildfires in southwestern Idaho (43° 35' N, 115° 42' W). The Foothills Burn (89 159 ha) was created in 1992 by a mixed-severity wildfire, and about 40% of snags over 23 cm in diameter at breast height (dbh) were harvested after the fire. The Star Gulch Burn (12 467 ha), in 1994, was also a mixed-severity wildfire and bordered the Foothills Burn to the north. The

Star Gulch Burn contained two 400-ha management units that were excluded from salvage logging (Saab et al. 2007). Portions of the burn outside of these two units were selectively logged to various degrees based on slope aspect and fire intensity (U.S. Department of Agriculture [USDA] 1995). Pre-fire vegetation in both areas was similar and dominated by ponderosa pine and Douglas-fir (*Pseudotsuga menziesii*) with occasional quaking aspen (*Populus tremuloides*) and subalpine fir (*Abies lasiocarpa*). Elevation ranged from 1100 to 2300 m, slope from 3 to 98%. Pre-logging snag density, pre-fire crown closure, and fire severity of the two burns was similar (Saab et al. 2007).

STUDY DESIGN

We used 100 radio-telemetry locations and four fixed-kernel home-range (Worton 1989) polygons reported in Dudley and Saab (2007) to predict foraging-habitat selection at multiple spatial scales for four adult male Black-backed Woodpeckers during the post-fledging period. Telemetry data were collected in 2000 and 2002 (see Dudley and Saab 2007 for details), which corresponded to 6 and 8 years following fire. Telemetry locations represented the first tree, snag, or log where a male was observed foraging during standardized observation periods. Foraging behaviors included those commonly described for woodpeckers (e.g., scaling, pecking, and drilling bark; Remsen and Robinson 1990) and included successful (71% of observations), unsuccessful (17%), and unknown-outcome (12%) foraging bouts. During observations, males attended at least one fledgling.

We assessed foraging-habitat selection with a use-availability study design (Manly et al. 2002, Lele and Keim 2006). We randomly selected 25 radio-telemetry locations of each male to represent selected (used) foraging habitat (38–60% of each male's radio-telemetry locations; Dudley and Saab 2007) for each year from September to November 2000 and October to November 2002. Logistical constraints allowed field sampling (vegetation characteristics; see below) at a maximum of 25 use locations for each male. We generated 25 random locations within each bird's 100% fixed-kernel home range to represent available foraging habitat. We used 100% fixed-kernel home ranges to maximize our potential to characterize habitat use from the entire suite of telemetry locations rather than from a smaller estimate (e.g., 95% utilization distribution; Erickson et al. 2001). We used a global positioning system device to navigate to each random location and selected the nearest tree or snag within 15 m and >8 cm dbh to serve as the center of a sample plot. We set 8 cm dbh as a lower cutoff because birds were observed only twice on trees or snags of smaller diameter (range of foraging trees 5.2–129.2 cm dbh, $n = 192$; this study). If no trees or snags were within 15 m of the random coordinate, we chose a new coordinate until we arrived at 25 random locations for each male. At each location, we measured several tree- and

plot-level variables within a 0.04-ha circular plot centered on the foraging or random tree (Table 1).

We derived coarse-scale covariates from Landsat Thematic Mapper satellite imagery. We obtained pre-fire (22 September 1991) 30-m-resolution classified images (maps) of our study area representing categories of vegetation and tree-crown closure (Johnson et al. 2000). Vegetation types included Douglas-fir, ponderosa pine, ponderosa pine/Douglas-fir mix, and lesser amounts of subalpine fir and quaking aspen. Tree-crown-closure categories were low (>10–40%), moderate (>40–70%), and high (>70%). Overall classification accuracy was 79% for vegetation type and 78% for crown closure (Johnson et al. 2000). We subsequently generalized each map by passing a 3×3 -pixel window over the map and assigning the center pixel the value of the most frequent class (Booth and Oldfield 1989).

We used Burned Area Reflectance Classification-Adjustable (BARCA) (Hudak et al. 2004) maps to represent a continuous index of burn severity within the study area. These maps were developed from pre-fire (22 September 1991) and post-fire (27 September 1993—Foothills Fire, 1 September 1995—Star Gulch Fire) Landsat Thematic Mapper images. As with the vegetation-type and crown-closure maps, we generalized the BARCA map by passing a 3×3 -pixel window over the map and assigning the median value to the center pixel. All map products were originally processed by the U.S. Forest Service's Remote Sensing Applications Center (<http://www.fs.fed.us/eng/rsac/>).

We used landscape-metrics software (FRAGSTATS; McGarigal et al. 2002) to calculate coarse-scale patch attributes associated with the 25 used and 25 available locations in each male's home range (Table 1). By default, all random (available) locations fell within conifer vegetation types (i.e., we considered open areas as not available for foraging).

STATISTICAL ANALYSES

We used resource-selection probability functions (Lele and Keim 2006) in an information-theoretic framework (Burnham and Anderson 2002) to identify habitat features that best distinguished between foraging and random locations. On the basis of previous work (e.g., Caton 1996, Hoffman 1997, Russell et al. 2007, Saab et al. 2009; Table 2), we developed 11 a priori candidate models of the resource-selection probability function that we considered biologically relevant to foraging. Inclusion of covariates in models depended on covariate associations with tree mortality and whether those associations were likely to promote beetle colonization and the woodpeckers' subsequent foraging. We mutually excluded from models covariates that were moderately to highly correlated (Pearson $r \geq 0.70$) and retained only those covariates appropriate to our a priori hypotheses and relevant to management. For example, we considered tree diameter as a covariate because beetle reproduction is usually greater in trees of larger diameter,

TABLE 1. Covariates used to model foraging habitat selection by Black-backed Woodpeckers in southwestern Idaho, 2000 and 2002.

Spatial scale and covariate	Description
Fine scale (tree-level)	
Tree diameter _{tree}	Diameter (cm) at breast height (dbh, 1.37 m) of the tree on which the bird foraged or single random tree
Percentage charred	Percentage of the tree's height that is charred by fire for the tree on which the bird foraged or single random tree
Fine scale (plot-level ^a)	
Percentage pine	Percentage of live and/or dead conifers ≥ 8 cm dbh that are ponderosa pine.
Tree diameter _{plot}	Mean diameter (cm) of conifers ≥ 8 cm dbh.
Tree density	Density (number per plot) of conifers ≥ 8 cm dbh.
Coarse scale (224–778 ha)	
Patch size	Area (ha) of the patch (McGarigal et al. 2002) containing the foraging or random location. Patches were defined by their unique combination of conifer vegetation type and crown closure derived from pre-fire Landsat imagery (e.g., ponderosa pine/low crown closure) (Johnson et al. 2000).
Proximity	Proximity index (McGarigal et al. 2002) of the focal patch that contains the foraging or random location to all other patches in the home range, classified as having moderate (>40 – 70%) or high ($>70\%$) crown closure, derived from pre-fire Landsat imagery (Johnson et al. 2000). Smaller index values suggest patches are more isolated and fragmented than patches assigned larger index values.
Burn severity	Burn-severity index of the pixel that contains the foraging or random location, derived from change in normalized burn ratio of pre-fire and post-fire Landsat imagery (Hudak et al. 2004). Index values range from 0 to 255 and correspond to a burn-severity continuum ranging from unburned to high, respectively.

^aSample plot was a circle of radius 11.3 m (0.04 ha) centered on the tree in which the bird foraged or random tree.

TABLE 2. A priori hypotheses for predicting Black-backed Woodpecker foraging trees at multiple spatial scales in southwestern Idaho, 2000 and 2002. See Table 1 for explanation of variable names.

Spatial scale and model prediction	Covariates
Single scale	
<i>Fine/tree</i> : Black-backed Woodpeckers will forage on large-diameter trees	Tree diameter _{tree}
<i>Fine/tree</i> : Black-backed Woodpeckers will forage on trees with high percentage of the bole scorched	Percentage charred
<i>Fine/tree</i> : Black-backed Woodpeckers will forage on large-diameter trees with high percentage of the bole scorched	Tree diameter _{tree} , percentage charred
<i>Fine/plot</i> : Black-backed Woodpeckers will forage in ponderosa pine patches	Percentage pine
<i>Fine/plot</i> : Black-backed Woodpeckers will forage in ponderosa pine patches consisting of high densities of large diameter trees	Percentage pine, tree diameter _{plot} , tree density
<i>Coarse</i> : Black-backed Woodpeckers will forage in large forest patches	Patch size
<i>Coarse</i> : Black-backed Woodpeckers will forage in close proximity to patches of moderate to high crown closure pre-fire and in forest patches with high burn severity	Proximity, burn severity
<i>Coarse</i> : Black-backed Woodpeckers will forage in large forest patches consisting of high burn severity that are in close proximity to prefire, moderate-to-high crown closures	Proximity, burn severity, patch size
Multi-scale	
<i>Tree and plot interaction</i> : Black-backed Woodpeckers will forage on large-diameter trees in patches of dense forest	Tree diameter _{tree} , tree density, tree diameter _{tree} \times tree density
<i>Tree, plot, and coarse</i> : Black-backed Woodpeckers will forage on large-diameter trees in ponderosa pine patches consisting of high densities of trees that are in close proximity to areas of moderate-to-high crown closure pre-fire	Tree diameter _{tree} , percentage pine, tree density, proximity
<i>Plot and coarse</i> : Black-backed Woodpeckers will forage in dense forest patches consisting of large-diameter trees that are in close proximity to areas of moderate-to-high crown closure pre-fire	Tree diameter _{plot} , percentage pine, tree density, proximity

owing to their thicker phloem than in trees of smaller diameter (Coulson 1979, Zhang et al. 1993, McHugh et al. 2003). This increase should translate into increased availability of prey to Black-backed Woodpeckers, which drill easily into the bark of trees. We considered tree density as a potential covariate because increasing tree density reduces phloem thickness, a measure of tree vigor, and may increase susceptibility to mortality when combined with other stressors (Amman et al. 1977). For these reasons, forest managers commonly incorporate tree diameter and density into systems rating insect hazards (Steele et al. 1996, Chojnacky et al. 2000).

We considered the percentage of tree charred and remotely sensed burn severity as fine- and coarse-scale covariates, respectively, because we recognize the potential role of fire in the life history of many beetle species (Evans 1971, McCullough et al. 1998, Saint-Germain et al. 2004a). Additionally, we included burn severity because it introduces a coarse-scale variable that is commonly used to inform postfire management (Lachowski et al. 1997, Miller and Yool 2002). After it is exposed to fire, a tree's mortality is related to a suite of factors (Hull Sieg et al. 2006, Keyser et al. 2006, Hood et al. 2007). We used percentage of the tree charred as a surrogate for damage to the cambium affecting the tree's defense from beetle attack. Similarly, we relied on remotely sensed burn severity as an index to tree-crown damage caused by fire at the coarse spatial scale (Wallin et al. 2003). In contrast, we did not use decay of individual trees in our models because it was generally too coarse of an indicator of beetle activity in our study area.

We considered percentage ponderosa pine at the plot level as a fine-scale covariate because the bark of ponderosa pine is somewhat thinner than that of Douglas-fir, potentially making it more susceptible to fire injury and subsequent beetle attack (Hood et al. 2007). Furthermore, during logging, ponderosa pine is often favored over Douglas-fir, so knowing its importance to Black-backed Woodpecker foraging would be informative to forest managers.

We used patch size and proximity to moderate and high crown closures as remotely sensed, coarse-scale indices of landscape pattern that may influence bark beetle distributions (cf. Bentz et al. 2010) as well as Black-backed Woodpecker foraging (Li and Wu 2004). We defined patches as regions with unique combinations of cover type and crown closure, which allowed us to capture the variability in forest structure at a level on which beetle prey respond. Because Black-backed Woodpeckers are highly mobile (Dudley and Saab 2007), we considered proximity to patches of moderate and high crown closure as an influence of patch arrangement on foraging. Consequently, both the size and arrangement of suitable patches might have important management implications.

We used R version 2.12.0 (R Development Core Team 2010) to fit stratified logistic resource-selection probability functions for forage-tree probability where each bird

was considered a stratum in the likelihood function (Lele and Keim 2006). Thus we modeled habitat selection as a weighted distribution and constrained available habitat to depend on home range because home ranges of birds did not overlap during the study period (Dudley and Saab 2007). Because used/available forage trees were our unit of analysis, and we sampled from the home ranges of four birds, the scope of inference for this analysis is limited to those trees within the combined home ranges of radio-marked birds. Our results are suggestive for ponderosa pine forests in general, but we cannot infer to trees elsewhere in the Black-backed Woodpecker's range.

We confirmed goodness of fit and evaluated potential overdispersion of the most highly parameterized model to assure relative plausibility of ranking candidate models in the model-selection framework. We constrained models to ≤ 5 estimated parameters (four covariates) to avoid overparameterization (Burnham and Anderson 2002). We used Akaike's information criterion adjusted for small sample size (AIC_c) to rank candidate models (Hurvich and Tsai 1989) and considered models within four AIC_c units of the model with lowest AIC_c as plausible (Burnham and Anderson 2002). We calculated the relative weight of evidence (i.e., Akaike weight) for each model as the best approximating model (Burnham and Anderson 2002). We assessed the performance of the highest-ranked model with Cohen's κ statistic (Manel et al. 2001), and we constructed 95% confidence intervals to evaluate parameter estimates for each covariate in the highest-ranked model. We considered parameters with confidence intervals that excluded zero to be important factors in the Black-backed Woodpecker's selection of foraging trees.

RESULTS

The most parameterized model (resource-selection probability function) had adequate fit ($\chi^2 = 13.7$, $P = 0.09$) and acceptably low dispersion ($\hat{c} < 1.6$). Model selection yielded one plausible model (Akaike weight 0.99), a cross-scale model containing tree- and plot-level covariates and their interaction (Table 3). Foraging-tree diameter and plot-level tree density constituted the top-ranked model, and, given the data, no other models (at fine or coarse scale) were plausible ($\Delta AIC_c > 17$; Table 3). Thus plot-level percentage ponderosa pine trees or snags, plot-level tree diameter, tree-level percentage tree charred, coarse-scale burn severity, patch size, and pre-fire proximity to patches of moderate to high crown closure were not supported in any plausible model.

Confidence intervals for top-ranked model covariates suggested that fine-scale foraging-tree diameter, plot-level tree density, and their interaction all contributed significantly to model fit (Table 4). Cohen's κ for the top-ranked model suggested moderate model performance ($\kappa = 0.4$). Generally, the probability of Black-backed Woodpeckers foraging on a tree

TABLE 3. Model-selection results for assessing the relationship between fine- (tree and plot levels) and coarse-scale variables and Black-backed Woodpecker foraging in southwestern Idaho, 2000 and 2002. Candidate models are ranked from most ($\Delta\text{AIC}_c = 0$) to least plausible; K is the number of parameters. See Table 1 for explanation of variables' names.

Candidate model	$-2(\log$ likelihood)	K	ΔAIC_c^a	Akaike weight
Tree diameter _{tree} + tree density + tree diameter _{tree} \times tree density	-96.94	4	0.00	0.99
Tree diameter _{tree} + plot percentage pine + tree density + pixel proximity	-81.71	5	17.36	0.00
Tree diameter _{plot} + plot percentage pine + tree density + pixel proximity	-80.29	5	18.78	0.00
Tree diameter _{plot} + plot percentage pine + tree density	-71.22	4	25.72	0.00
Pixel patch size + pixel proximity + pixel burn severity	-29.40	4	67.54	0.00
Tree diameter _{tree} + tree percentage charred	-23.75	3	71.09	0.00
Tree percentage charred	-15.98	2	76.77	0.00
Pixel patch size	-15.83	2	76.93	0.00
Tree diameter _{tree}	-15.12	2	77.63	0.00
Plot percentage pine	-6.04	2	86.71	0.00
Pixel proximity + pixel burn severity	-7.21	3	87.62	0.00

^aAkaike's information criterion adjusted for small sample size; minimum $\text{AIC}_c = -86.63$.

TABLE 4. Mean, standard error (SE), and 95% confidence limits (CL) for parameter estimates from the highest-ranking model (Table 3) for predicting foraging-tree habitat for Black-backed Woodpeckers in southwestern Idaho, 2000 and 2002.

Parameter	Mean	SE	95% CL
Intercept	-1.788	0.653	-3.068, -0.508
Tree diameter _{tree}	-0.041	0.016	-0.072, -0.010
Tree density	-0.179	0.067	-0.310, -0.048
Tree diameter _{tree} \times tree density	0.015	0.003	0.009, 0.021

increased with the interaction between the tree's diameter and tree density (Fig. 1, Table 4).

DISCUSSION

We provide new information pertaining to the Black-backed Woodpecker's selection of foraging habitat, although our results are limited in scope of inference to trees encompassed by the combined home ranges of four individuals. Our model suggests that foraging Black-backed Woodpeckers may first select habitats with dense trees, then select individual trees of larger diameter. This mechanism may parallel that of host selection by their main prey items (i.e., bark and wood-boring beetles; Zhang et al. 1993, Saint-Germain et al. 2004a, b). We are not aware of a previously reported interaction between habitat covariates at multiple spatial scales (i.e., foraging-tree and plot levels).

Foraging locations were positively associated with foraging-tree diameter and tree densities, supporting our predictions regarding selection for large tree diameters and high tree densities. This is consistent with other studies reporting that Black-backed Woodpeckers forage on large-diameter

trees (Powell 2000, Tremblay et al. 2010) and in habitats with dense trees (Nappi et al. 2003, Hanson and North 2008). Furthermore, our results support previously reported conclusions that Black-backed Woodpeckers forage in larger-diameter, prey-rich trees, regardless of prey density at the patch level (Powell 2000, Nappi et al. 2003). The density of trees surrounding larger-diameter trees may help to promote successful beetle colonization and reproduction by facilitating death or decline of the larger trees beetles prefer. For example, within burned areas, large-diameter trees in patches of dense forest may be killed directly as fire is more easily carried in such patches than in relatively open patches where trees are only lightly scorched. These large-diameter trees would thus be readily available for beetle colonization but presumably deteriorate with time (Hanks 1999). At 6 and 8 years after fire, we often observed radio-tagged birds foraging low on the trunks and deep in the sapwood of such trees (unpubl. data). Similarly, large-diameter trees that survive wildfire may become stressed because of increased competition with remaining live trees, resulting in delayed mortality of the larger-diameter trees beetles prefer (Nappi et al. 2010). Such trees represent new recruitment of prey in older burns and a shift in Black-backed Woodpecker foraging that is more uniformly distributed on the tree bole. These patterns may be more pronounced in older burns when beetle populations are presumably reduced and more patchily distributed than in more recently burned forests (≤ 5 years after fire) (Powell 2000, Covert-Bratland et al. 2006, Saint-Germain et al. 2008, Nappi et al. 2010).

In contrast to Hanson and North (2008), we did not find support for our prediction that Black-backed Woodpeckers should forage more in severely burned trees than at random locations. Time since fire is likely a factor in the differences

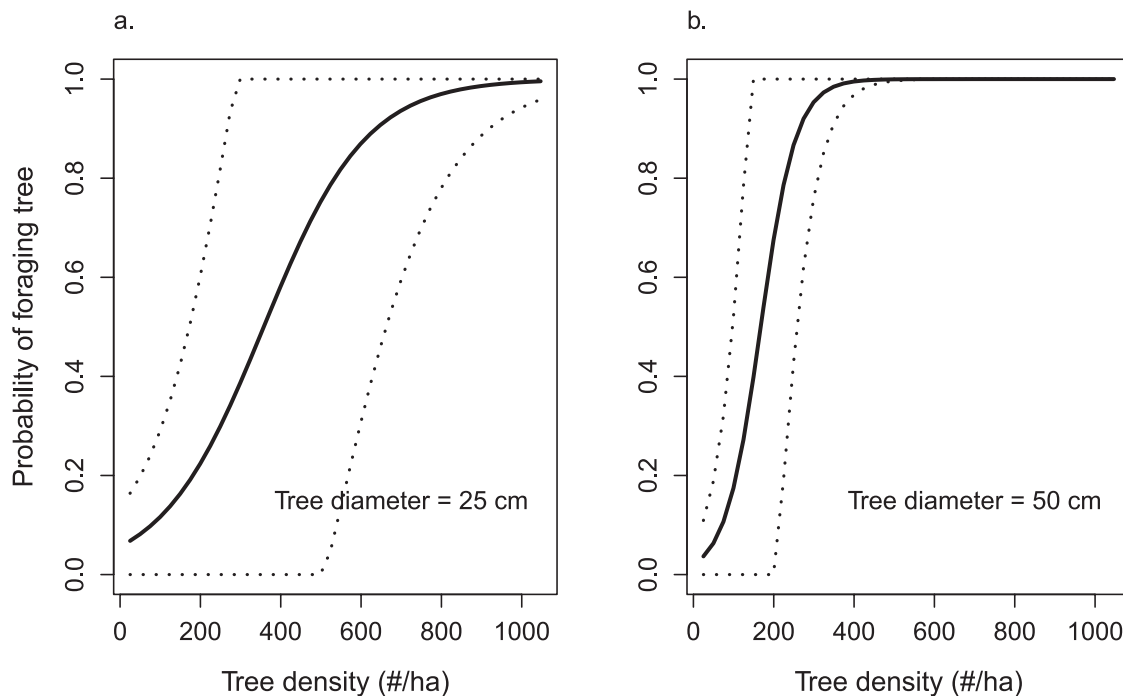


FIGURE 1. Probability of a tree being used for foraging by Black-backed Woodpeckers at varying tree densities and constant foraging-tree diameter (a, 25 cm; b, 50 cm) at breast height in burned forests of southwestern Idaho, 6 and 8 years after wildfire, 2000 and 2002. Dotted lines represent 95% confidence limits.

in our results. Our study was conducted 6–8 years post-fire, that of Hanson and North (2008) 1–5 years post-fire. This difference in time may represent a period when snags deteriorate and trees become less suitable for beetle colonization (Hanks 1999, Nappi et al. 2010). Our results, however, are consistent with patterns of Hairy Woodpeckers (*Picoides villosus*) foraging in burns of different ages. At 6–7 years after wildfire, Covert-Bratland et al. (2006) found that Hairy Woodpeckers did not use severely burned areas more than moderately burned areas, as they did at 2–3 years after wildfire.

In burns of moderate-to-high severity, populations of bark and wood-boring beetles peak around 2–3 years post-fire (Saint-Germain et al. 2004a, Covert-Bratland et al. 2006). By 6–8 years after fire, beetles have largely dispersed from the interior of severely burned areas and have potentially attacked weakened trees, attracting beetle-foraging woodpeckers (cf. Covert-Bratland et al. 2006, Dudley and Saab 2007). These weakened trees may occur in less severely burned patches at the periphery of the burn or in unburned patches damaged by weather. Such a scenario might explain observations of radio-tracked birds foraging in adjacent unburned forests (Dudley and Saab 2007).

Foraging locations were positively associated with tree densities, consistent with previous findings for the Black-backed Woodpecker's nest sites in this study area (Saab et al. 2009). Some areas within the home ranges of our birds were partially logged, and the mean densities of trees and snags

available to them were potentially quite variable (Table 5). Because tree densities were positively associated with foraging locations, birds may avoid logged areas when tree and snag densities are reduced (Koivula and Schmiegelow 2007, Saab et al. 2007), especially if logging precedes beetle colonization.

We did not find evidence that tree species was important to Black-backed Woodpecker foraging. Similarly, tree species was not important for discriminating between nest and non-nest habitats in our study area (Saab et al. 2009). This suggests that Black-backed Woodpeckers are not limited by species-specific tree patches for nesting or foraging (Murphy and Lehnhausen 1998, Powell 2000, Nappi et al. 2003). Maintaining tree-species diversity within forest patches will likely support a greater diversity of beetles over time, thus remaining suitable for woodpecker foraging and contribute to population persistence in burned forests (Hoyt and Hannon 2002, Saint-Germain et al. 2004a).

The ability of burned areas to support Black-backed Woodpeckers may be compromised at 6–8 years following fire. Indeed, the birds' density in our study area began to decline 4–5 years after fire (Saab et al. 2007). In boreal landscapes, Nappi et al. (2010) found Black-backed Woodpeckers using burns up to 8 years post-fire but absent from burns 16 and 17 years post-fire (Hoyt and Hannon 2002). In the absence of fire, beetle-killed and mature unburned forests may support lower numbers of Black-backed Woodpeckers (Setterington

TABLE 5. Mean (SE) summary statistics for variables used to model foraging-habitat selection of four male Black-backed Woodpeckers at multiple spatial scales during the post-fledging period in southwestern Idaho, 2000 and 2002; $n = 25$ for each male, $n = 100$ for all males combined. Results for random locations are in bold. See Table 1 for descriptions of variables.

Spatial scale and variable	Male 1	Male 2	Male 3	Male 4	All males
Tree level					
Tree diameter (cm)	32.8 (3.4)	63.6 (4.4)	38.8 (3.1)	40.5 (3.2)	43.9 (2.1)
	31.5 (3.0)	53.6 (4.5)	36.7 (5.2)	36.5 (3.8)	39.6 (2.2)
Percentage charred	7.6 (4.1)	48.2 (7.1)	14.7 (4.2)	65.6 (7.2)	34.0 (3.7)
	20.7 (7.4)	58.1 (7.0)	23.1 (8.1)	80.5 (6.0)	45.6 (4.3)
Plot-level (0.04 ha)					
Percentage pine	37.4 (7.5)	0.2 (0.2)	59.9 (8.0)	41.8 (8.6)	34.8 (4.1)
	47.4 (7.6)	7.3 (3.2)	57.4 (9.2)	60.5 (8.8)	43.2 (4.3)
Tree diameter (cm)	24.8 (1.2)	45.8 (2.4)	30.9 (1.8)	34.4 (2.2)	34.0 (1.2)
	28.1 (2.7)	49.5 (4.4)	30.0 (3.2)	36.2 (2.9)	36.0 (1.9)
Tree density (ha^{-1})	388.9 (42.4)	211.4 (26.5)	371.9 (33.1)	239.3 (31.8)	302.9 (18.5)
	306.1 (52.1)	104.7 (18.4)	283.2 (53.5)	139.6 (23.7)	208.4 (21.7)
Coarse scale (224–778 ha)					
Patch size (ha)	10.5 (1.9)	5.0 (0.8)	5.8 (1.3)	16.8 (3.7)	9.5 (1.2)
	5.9 (2.0)	2.6 (0.5)	5.6 (1.5)	16.3 (3.7)	7.6 (1.2)
Proximity index	1205.8 (54.4)	267.0 (26.2)	287.4 (26.6)	1511.3 (45.1)	817.9 (58.8)
	1430.5 (132.5)	273.4 (33.9)	230.4 (27.1)	1278.0 (73.6)	803.1 (67.9)
Burn-severity index	105.0 (4.1)	148.0 (7.4)	90.9 (2.8)	165.9 (2.9)	127.5 (3.8)
	104.3 (5.5)	152.2 (6.6)	101.4 (6.8)	162.0 (4.0)	129.9 (4.0)

et al. 2000, Bonnot et al. 2008, Saint-Germain et al. 2008, Tremblay et al. 2010). Low numbers of Black-backed Woodpeckers continued to nest 10 years after fire (Saab et al. 2007), but opportunities to forage within the burned area may have been diminished from those early after the fire. The reduction in foraging opportunity may be due to a qualitative and quantitative loss of trees hosting their beetle prey (Russell et al. 2006, Covert-Bratland et al. 2006, Saint-Germain et al. 2008).

MANAGEMENT IMPLICATIONS

We suggest that retention of patches containing high densities of trees of large diameter will reserve habitats for foraging Black-backed Woodpeckers within 8 years after wildfire, which supports earlier recommendations for reserving their nesting habitat (Russell et al. 2007, Saab et al. 2009). Additionally, our results suggest that forest patches may provide similar foraging opportunities even though they contain different combinations of tree densities and diameters (Fig. 1). For example, in one patch large-diameter trees may be surrounded by few trees, whereas another patch may contain trees of smaller diameter surrounded by high tree densities. Yet these two patches may be qualitatively similar in providing beetle prey. This interaction between diameter of foraging trees and density of surrounding trees may prove important in heavily managed forests and warrants further investigation. Although Black-backed Woodpeckers nest and forage in multiple species of trees, we caution against selective removal of focal tree species when these trees occur in mixed patches. Furthermore, because our birds

foraged in adjacent unburned forests, conservation of patches containing weakened trees on the periphery of wildfires may be critical for extending the longevity of habitats suitable for foraging Black-backed Woodpeckers in dry coniferous forests of the interior western U.S.

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